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Micromotional Studies of Utricular and Canal Afferents

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I. Description of Research

The long-range goal of this research was to refine our understanding of the sensitivity of the vestibular components of the ear to very-low-amplitude motion, and especially the role of gravity in this sensitivity.

We focused on the American bullfrog-- a common animal subject for vestibular sensory research. Our principal experimental method was to apply precise, sinusoidal microrotational stimuli to an anesthetized animal subject, to record the resulting responses in an individual vestibular nerve fiber from the intact ear, and to use intracellular dye to trace the fiber and thus identify the vestibular sensor that gave rise to it. In this way, we were able to identify specific micromotional sensitivities and to associate those sensitivities definitively with specific sensors. Furthermore, by recording from nerve fibers after they leave the intact inner-ear cavity, we were able to achieve these identifications without interrupting the delicate micromechanics of the inner ear. We were concerned especially with the relative roles of the utricle and the anterior semicircular canal in the sensing of microrotational motion of the head about horizontal axes, and with the role of gravity in mediating that sensing process in the utricle. The functional characterization of individual nerve fibers was accomplished with a conventional analytical tool-- the cycle histogram, in which the nerve impulse rate was plotted against the phase of the sinusoidal stimulus.

II. Accomplishments

Using intracellular dye to trace functionally characterized vestibular axons to their peripheral origins, we definitively separated anterior vertical canal axons from utricular axons, and demonstrated conclusively that there is a sizable population of utricular striolar axons that mimic the rotational sensitivity usually attributed to anterior vertical canal axons. For small-amplitude, low-frequency rotations about horizontal axes, the firing rate in a subset of utricular axons follows rotational velocity more faithfully (in both phase and amplitude) than does that in any of the vertical canal axons we studied. We have demonstrated definitively that the stimulus for this faithful representation of rotational velocity is the RATE OF CHANGE of the PROJECTION OF THE GRAVITY VECTOR onto the utricular surface; and NOT centripetal acceleration of the otoconial mass of the utricle. This faithful rotational velocity response spans a very large part of the normal motional range of the head-- from approximately 0.1 Hz to more than 4.0 Hz.

Scanning electron microscopy studies have shown that the sensory surface (crista) of the anterior semicircular canal is divided into five regions, characterized by different distributions of sensory hair bundles (the transduction apparatus). The hair bundles have been classified as types A (those with the longest stereocilia equal in length to the

kinocilium) and B (those with the longest stereocilia being less than 2/3 as long as the kinocilium. The peripheral (planar) regions on each side have only type B bundles, densely distributed. Between the two planar regions is the ridge. The central region of the ridge has hair bundles with densities and has only types A bundles, also densely distributed. The regions of the ridge lying between this central region and the planar regions have types A and B bundles, but sparsely distributed. Individual axons tend to innervate either the ridge regions or a planar region, but not both. Axons from the planar regions consistently have conspicuously lower gain and more periodic (less random) spontaneous firing than those from the ridge regions. On the other hand, no differences in gain or regularity of firing was found between the axons innervating the central region of the ridge and those innervating the other two ridge regions. Thus, gain and regularity of firing do not appear to be determined by hair bundle type.

In principle, if the spontaneous firing of a nerve fiber were perfectly regular, then even the smallest stimulus-induced variation in firing pattern would be detectable. Irregularity of firing makes detection more difficult, and can be interpreted as being equivalent to noise in the channel. Taking the rms deviation of the instantaneous firing rate from its mean to be the equivalent noise amplitude, we found that the stimulus amplitude required to exceed the nerve-fiber's noise level was independent of where the fiber arose. Those from the ridge exhibited higher gain, but also higher noise; those from the planar regions exhibited lower gain, but also lower noise. In terms of signal detectability, both types of fibers were approximately equivalent.

III. Significance of the Accomplishments

It is well known that the human vestibulo-ocular reflex operates very well for head rotations that are a small fraction of a degree. Traditionally, the sensors responsible for this reflex have been assumed to be the semicircular canals. The otoconial organs of mammals have been considered sensors of translational motion and of head orientation relative to gravity. Our observations of gravity-mediated rotational velocity sensitivity in the frog casts serious doubt on this traditional view. Furthermore, our results suggest that serious deficits in rotational motion sensitivity could occur in microgravity environments.

IV. Publications

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